

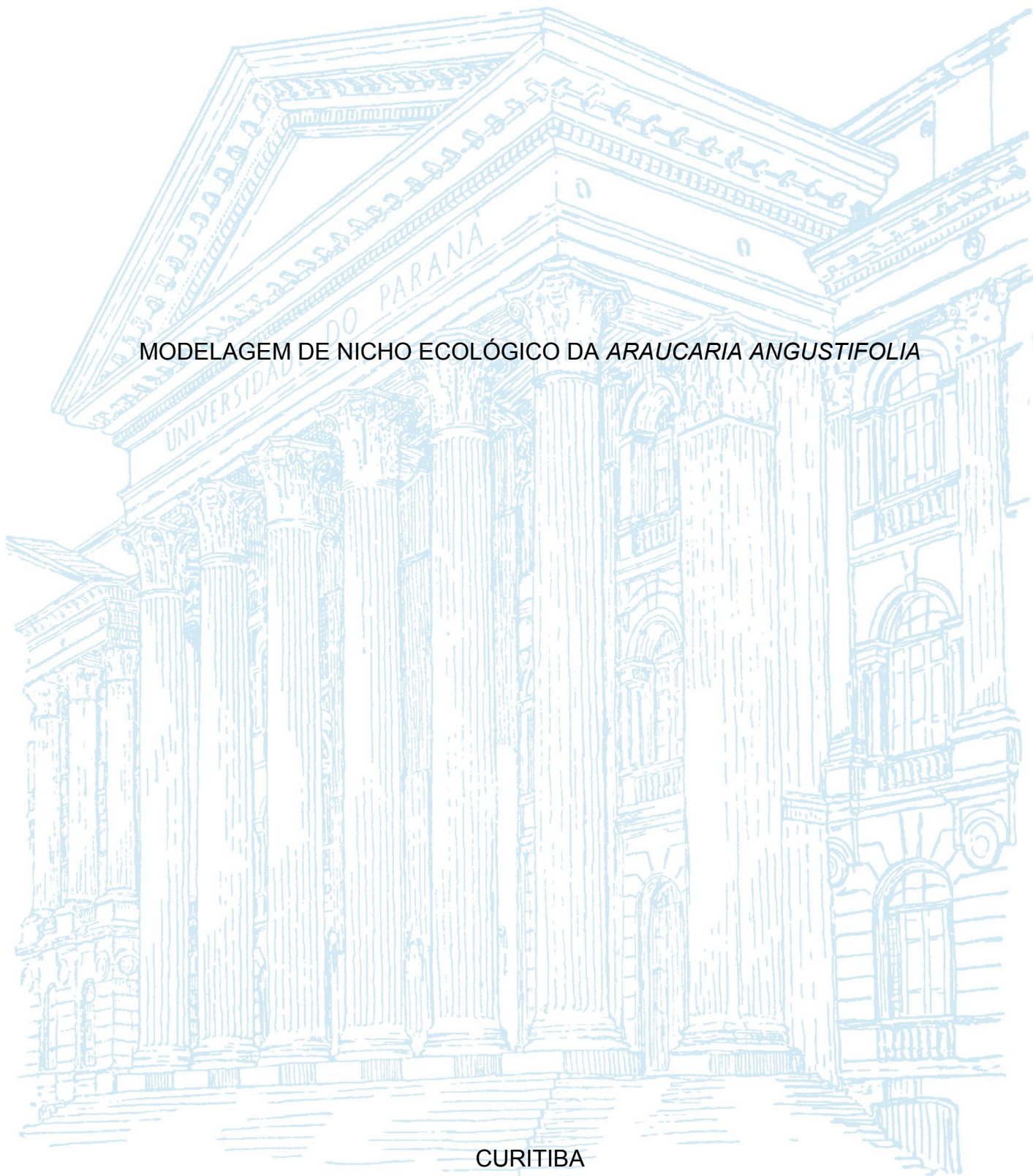
UNIVERSIDADE FEDERAL DO PARANÁ

GIULLIANA BAGGIO BERNARDINIS

MODELAGEM DE NICHU ECOLÓGICO DA *ARAUCARIA ANGUSTIFOLIA*

CURITIBA

2021



GIULLIANA BAGGIO BERNARDINIS

MODELAGEM DE NICHOS ECOLÓGICO DA *ARAUCARIA ANGUSTIFOLIA*

Dissertação apresentada como requisito parcial à obtenção do título de Mestre, Curso de Botânica, Setor de Ciências biológicas, Universidade Federal do Paraná.

Orientador: Victor Pereira Zwiener

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No dia dezoito de junho de dois mil e vinte e um às 14 horas, na sala <https://meet.google.com/osc-bsdg-vpo>, VIDEOCONFERÊNCIA, foram instaladas as atividades pertinentes ao rito de defesa de dissertação da mestranda **GIULLIANA BAGGIO BERNARDINIS**, intitulada: **Modelagem de Nicho Ecológico da Araucaria angustifolia**, sob orientação do Prof. Dr. VICTOR PEREIRA ZWIENER. A Banca Examinadora, designada pelo Colegiado do Programa de Pós-Graduação em BOTÂNICA da Universidade Federal do Paraná, foi constituída pelos seguintes Membros: VICTOR PEREIRA ZWIENER (UNIVERSIDADE FEDERAL DO PARANÁ), SANTIAGO JOSE ELIAS VELAZCO (UNIVERSITY OF CALIFORNIA, DEPARTMENT OF BOTANY AND PLANT SCIENCES), MARCIO VERDI (INSTITUTO DE PESQUISAS JARDIM BOTANICO DO RIO DE JANEIRO). A presidência iniciou os ritos definidos pelo Colegiado do Programa e, após exarados os pareceres dos membros do comitê examinador e da respectiva contra argumentação, ocorreu a leitura do parecer final da banca examinadora, que decidiu pela APROVAÇÃO. Este resultado deverá ser homologado pelo Colegiado do programa, mediante o atendimento de todas as indicações e correções solicitadas pela banca dentro dos prazos regimentais definidos pelo programa. A outorga de título de mestre está condicionada ao atendimento de todos os requisitos e prazos determinados no regimento do Programa de Pós-Graduação. Nada mais havendo a tratar a presidência deu por encerrada a sessão, da qual eu, VICTOR PEREIRA ZWIENER, lavrei a presente ata, que vai assinada por mim e pelos demais membros da Comissão Examinadora.

Curitiba, 18 de Junho de 2021.

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em BOTÂNICA da Universidade Federal do Paraná foram convocados para realizar a arguição da dissertação de Mestrado de **GIULLIANA BAGGIO BERNARDINIS** intitulada: **Modelagem de Nicho Ecológico da Araucaria angustifolia**, sob orientação do Prof. Dr. VICTOR PEREIRA ZWIENER, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 18 de Junho de 2021.

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MARCIO VERDI

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Em memória a meu grande parceiro, Spyke. Obrigada por ter existido.

“What is grief, if not love persevering?” – Vision

(Wandavision, 2021)

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“ . . . earth and life evolve together,”

Léon Croizat (1894–1982)

RESUMO

A *Araucaria angustifolia* é um pinheiro nativo do Brasil, Paraguai e Argentina, que devido a exploração excessiva, fragmentação de habitats e outros fatores está em perigo de extinção. Esta árvore tem grande importância ecológica e nomeia todo o ecossistema a qual pertence, a Floresta com Araucaria. O objetivo desta dissertação foi de estimar a distribuição geográfica da espécie e potenciais alterações em decorrência dos efeitos das mudanças climáticas projetadas para o ano de 2050. Também buscou-se verificar se as unidades de conservação atuais serão eficazes, acomodando áreas de potencial distribuição no presente e em diferentes cenários futuros. A metodologia empregada se baseou na modelagem de nicho ecológico, com o algoritmo Maxent, uma técnica utilizada para estimar as condições favoráveis e projetar a distribuição geográfica baseando-se na correlação de dados empíricos sobre ocorrência de espécies com variáveis preditoras. Foi estimada a área de acessibilidade com modelos de dispersão e adequabilidade climática e foi realizada uma avaliação das incertezas das previsões de distribuição. A espécie terá a área de distribuição potencial reduzida de 45 a 56% dependendo do cenário (SSP2-4.5 e SSP5-8.5). Além disso mais de 52,36% - 73,51% das unidades de conservação atuais não terão mais um clima adequado para a sobrevivência da espécie. A maior fonte de variação do modelo encontradas nas análises realizadas é de Modelos de Circulação Climática. As áreas de campos com presença de Araucária serão pouco afetadas pelas mudanças climáticas, tornando-se áreas em potencial para novas medidas de proteção para espécie. Como a espécie terá sua distribuição exclusiva para o Brasil, sugere-se esforços para preservação da espécie nos estados do Rio Grande do Sul e Santa Catarina. Paraná é o estado mais afetado e perde maior parte de sua área de distribuição no cenário mais pessimista.

Palavras – chave: *Araucaria angustifolia* – Modelagem de Nicho Ecológico –

Distribuição da *Araucaria angustifolia* – Incertezas

ABSTRACT

Araucaria angustifolia is a native pine tree occurring in southern Brazil, Argentina and Paraguay, which due to overexploitation, habitat fragmentation and other factors is in currently critically endangered of extinction (IUCN). This tree has great ecological importance and names the entire ecosystem to which it belongs, the "Araucaria Forest". The objective of this dissertation was to estimate the potential distribution of the species and possible changes due to the effects of climate change projected for the year 2050. It was also aimed to verify if the current protected areas will be effective in the future, accommodating areas of potential distribution in different future scenarios. The methodology used was based on ecological niche modeling, a technique used to estimate favorable conditions and project the distribution based on the correlation of empirical data on the occurrence of species with predictor variables. The algorithm used was Maxent. The accessibility area was estimated with a dispersion model and climatic suitability, and an evaluation of the uncertainties of the distribution predictions were made. The species will have its potential distribution range reduced in 45 to 56% depending on which scenario (SSP2-4.5 and SSP5-8.5). Furthermore, more than 52.36% - 73.51% of current protected areas will be no longer climatically suitable for the species. The biggest source of model variation according with the realized analysis is from Climate Circulation Models. Grasslands areas with the presence of *Araucaria* will not be highly affected by climate change, becoming crucial areas for new protection measures for the species. Since the distribution of the species will become exclusive to Brazil, efforts to preserve the species are suggested in the states of Rio Grande do Sul and Santa Catarina. Paraná is the most affected state and loses most of its distribution area in the worst scenario.

Key words: *Araucaria angustifolia* – Ecological Niche modeling – *Araucaria* distribution – Uncertainties

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INTRODUÇÃO GERAL

As mudanças climáticas representam uma grande ameaça à biodiversidade e ao bem-estar humano, gerando preocupação em todo o mundo (IPBES, 2018; PECL et al., 2017). A sinergia entre mudanças climáticas somadas às mudanças de uso da terra, aumentam o risco de extinção de muitas espécies e perda de diversos processos e serviços ecossistêmicos mundiais (FAO, 2010; PEREIRA, 2010; ZWIENER et al., 2018; WRIGHT, 2005). Ainda assim, projeções futuras indicam que as mudanças climáticas se tornarão cada vez mais intensas com o passar do século XXI (TORRES & MARENGO, 2014).

O efeito de alterações climáticas já tem sido observado em uma variedade de grupos taxonômicos e funcionais (PARMESAN & YOHE, 2003). O aumento de temperatura pode impactar a distribuição de uma espécie, pois a temperatura é auto correlacionada no espaço, sendo que altitudes no nível do mar, ou abaixo, tenham condições de temperatura mais quentes, e condições mais frias em latitudes mais altas (LENOIR, et al., 2014). Muitas espécies estão expandindo sua distribuição em direção aos polos ou em regiões montanhosas em busca de climas mais amenos, e muitas podem se tornar vulneráveis ou serem extintas devido a diminuição de suas áreas de distribuição (BERGAMIN et al., 2019).

De maneira geral, a distribuição geográfica de uma espécie é permeada por um conjunto de fatores complexos redigidos durante sua história evolutiva (BROWN et al., 1996). Os principais fatores são: (i) condições abióticas, (ii) bióticas, e (iii) fatores históricos e estocásticos representados por padrões espaciais de dispersão (CURRIE et al., 2004; SOBERÓN & PETERSON, 2005). O conjunto multidimensional de fatores abióticos favoráveis a manutenção de populações de uma determinada espécie compõem o seu nicho fundamental (HUTCHINSON, 1957). Regiões que apresentam as respectivas condições abióticas correspondem a distribuição geográfica potencial da espécie na ausência de outros fatores restritivos como interações entre espécies e barreiras à dispersão (COLWELL & RANGEL, 2009). As espécies podem responder de maneira diferenciada aos seus limites de tolerância, podendo ter a população limitada por uma atividade predadora de outro organismo, ou tem dispersão facilitada por um polinizador específico (BARVE et al., 2011).

As áreas protegidas (PAs) são um dos grandes pilares para a conservação da biodiversidade em todo o mundo e são fundamentais para as políticas de adaptação e mitigação das mudanças climáticas (ELSEN et al., 2020; MAWDSLEY et al., 2009). PAs tem como objetivo de ajudar no amortecimento das mudanças nas condições ambientais, devem ser delimitadas a partir do rastreando de climas adequados que podem atuar como refúgios climáticos locais para espécies residentes (BELOTE et al., 2017; MAWDSLEY et al., 2009). Os locais das PAs são fixos e, conforme as mudanças climáticas, a eficácia de uma PA em manter as condições adequadas para a persistência de algumas espécies pode ser comprometida, prejudicando sua eficiência em garantir a persistência das espécies em longo prazo (ELSEN et al., 2020; HANNAH et al., 2007). Portanto, é primordial avaliar o papel do sistema de PAs na salvaguarda de condições adequadas para espécies ameaçadas de extinção. O julgamento crítico de sua eficácia em diferentes cenários de mudanças climáticas é decisivo para nortear as ações de gestão e políticas públicas (MACHADO et al., 2020; ZWIENER et al., 2017).

Em relação às PA, é fundamental entender a distribuição geográfica das espécies sob diferentes cenários ambientais para predizer sua adequabilidade no futuro, a fim de orientar os esforços de conservação em direção à sua persistência a longo prazo. Nesse sentido, a Modelagem de Nicho Ecológico (ENM) pode ajudar a desvendar como as mudanças climáticas futuras impactarão a distribuição da espécie abrangidas em PAs a partir da realização de previsões estatísticas de possíveis áreas de presença da espécie.

A ENM consiste em estimar a distribuição potencial da espécie, baseando-se na combinação de dados empíricos sobre ocorrência de espécies com variáveis preditoras, de forma a estabelecer um modelo estatístico (SOBERÓN & PETERSON, 2005). Uma vez estabelecido o ajuste, é possível estimar a distribuição em diferentes locais e/ou tempos (ANDERSON et al., 2003).

A *Araucaria angustifolia* (Bertol.) Kuntze - Araucariaceae (também conhecida como “Pinheiro-do-Paraná”) é uma espécie com grande valor ecológico, econômico e cultural, que se mantém classificada como “Criticamente em perigo” pela Lista Vermelha de Espécies Ameaçadas da União Internacional

para a Conservação da Natureza (IUCN) e “Em perigo” pela Lista Nacional Oficial de Espécies da Flora Brasileira Ameaçada de Extinção (MMA, 2014). Considerada a conífera nativa de maior importância econômica no Brasil, possui grande valor social, pois, além da sua extração em massa no período colonial brasileiro e do grande consumo regional de suas sementes (fatos que a colocaram no caminho da extinção), também foi um dos elementos utilizados para iniciar o Movimento Paranista no início do século XX, que tem como objetivo a construção de uma identidade regional paranaense. (CARVALHO & LAVERDI, 2015). A imagem da árvore e sua semente é utilizada em todo o estado, principalmente na capital, em adornos decorativos, tornando-a um símbolo regional (CARVALHO & LAVERDI, 2015).

O Pinheiro-do-Paraná ocorre no sul e sudeste do Brasil e no norte da Argentina, em uma área de aproximadamente 200.000 km². Contudo, devido ao extrativismo pela madeira e semente, a distribuição da espécie foi extremamente afetada, ocupando de 5 a 12% da área de distribuição natural original (ADAN et al., 2016).

Há estudos que indicam que a Floresta com Araucária se expande dentro de refúgios e áreas ribeirinhas nos biomas de Pampas, no Rio Grande do Sul, em um processo recente que se iniciou 4000 anos atrás, provavelmente em resposta à procura de um clima mais úmido. (BEHLING, 2002).

Nesse contexto, o presente estudo teve como objetivos: (i) estimar a distribuição geográfica da Araucária no presente e em cenários climáticos futuros (2050); (ii) avaliar e apresentar visualizações espacialmente explícitas da incerteza do modelo; (iii) avaliar as mudanças da distribuição potencial da espécie dentro das PAs.

Esperamos que a distribuição da Araucária seja principalmente influenciada pela precipitação, solo e fatores topográficos associados ao microclima. Outra expectativa é que a Araucária retraísse sua distribuição em geral, mas mantivesse áreas climáticas estáveis no sul do Brasil. Além disso, esperávamos que apenas uma pequena porcentagem da distribuição potencial esteja dentro das PAs e que essas áreas se tornem ainda menos eficazes em cenários futuros. Mais especificamente, também: (1) comparamos a contribuição

relativa dos fatores ambientais e as mudanças atuais no uso da terra para os padrões de distribuição; (2) avaliar a importância relativa das variáveis e configurações de parâmetros para as previsões do modelo; e (3) explorar as mudanças na adequação ambiental entre as localidades das populações remanescentes de Araucária.

REFERÊNCIAS BIBLIOGRÁFICAS

ADAN, N., ATCHISON, J., REIS, M. S., PERONI, N. Local Knowledge, Use and Management of Ethnovarieties of *Araucaria angustifolia* (Bert.) Ktze. in the Plateau of Santa Catarina, Brazil. **Econ Bot.** 70, 353–364. 2016.

ANDERSON, R.; LEW, D.; PETERSON, A. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*. v. 162 (30). 2003.

BARVE, N., BARVE, V., JIMENEZ-VALVERDE, A., LIRA-NORIEGA, A., MAHER, S. P., PETERSON, A. T., . . . VILLALOBOS, F. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. **Ecological Modelling**, 222, 1810–1819. 2011.

BEHLING, H. South and Southeast Brazilian Grasslands during Late Quaternary times: a synthesis. **Palaeoecology**. 177, 19 – 27. 2002.

BELOTE, R.T., DIETZ, M.S., JENKINS, C.N., MCKINLEY, P.S., IRWIN, G.H., FULLMAN, T.J., LEPPI, J.C. AND APLET, G.H. Wild, connected, and diverse: building a more resilient system of protected areas. **Ecol Appl**, 27: 1050-1056. 2017.

BERGAMIN, R. S., DEBASTIANI, V., JONER, D. C., LEMES, P.; GUIMARÃES, T., LOYOLA, R. D., MÜLLER, S. C. Loss of suitable climatic areas for *Araucaria* forests over time. **Plant Ecology & Diversity**. 12:2, 115-126. 2019.

BROWN, J. H.; STEVENS, G. C. & KAUFMAN, D. M. The Geographic Range: Size, Shape, Boundaries, and Internal Structure. **Annual Review of Ecology and Systematics** 27:597-623. 1996.

CARVALHO, A. I., LAVERDI, R. Espécie E Floresta: A Araucária Nos Discursos Ambientais E Na Produção De Sentidos Para As Florestas No Paraná. **Fronteiras: Journal of Social, Technological and Environmental Science** 4 (1), 224-48. 2015.

COLOMBO, A., JOLY, C. Brazilian Atlantic Forest *lato sensu*: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. **Braz. J. Biol.** 70(3). 697-708. 2010.

COLWELL, R.; RANGEL, T. Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*. 106(2). 2009.

CURRIE, D.; MITTELBAACH, G.; CORNELL, H.; FIELD, R.; GUÉGAN, J.; HAWKINS, B.; KAUFMAN, D., KERR, J., OBERDORFF, T., O'BRIEN, E., TURNER, J. Predictions, and tests of climate-based hypotheses broad-scale variation in taxonomic richness. **Ecology Letters**, 7, 1121 - 1134. 2004.

DULLINGER, S., GATTRINGER, A., THUILLER, W., MOSER, D., ZIMMERMANN, N., GUISAN, A., WILLNER, W., PLUTZAR, C., LEITNER, M., MANG, T., CACCIANIGA, M., DIRNBÖCK, T., ERTL, S., FISCHER, A., LENOIR, J., SVENNING, J., PSOMAS, A., SCHMATZ, D., ŠILC, U., HÜLBER, K. Extinction debt of high-mountain plants under twenty-first-century climate change. **Nature Climate Change**. 2. 619-622. 10.1038/nclimate1514. 2012.

ELSEN, P. R., MONAHAN, W. B., DOUGHERTY, E. R., MERENLENDER, A. M. Keeping pace with climate change in global terrestrial protected areas. **Sci Adv**. 6. 2020.

FAO. The State of Food and Agriculture 2009: Livestock in the Balance. **FAO**, Rome, 174 pp. Available at: <http://www.fao.org/publications/sofa/en/.2010>.

HANNAH, L., MIDGLEY, G., ANDELMAN, S., ARAÚJO, M., HUGHES, G., MARTINEZ-MEYER, E., PEARSON, R. AND WILLIAMS, P. Protected area needs in a changing climate. **Frontiers in Ecology and the Environment**, 5: 131-138. 2007.

HUTCHINSON, G.E. concluding remarks. **Cold Spring Harbor Symposia on Quantitative Biology**, 22, 415-427. 1957.

IPBES. The IPBES regional assessment report on biodiversity and ecosystem services for the Americas. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. 2018.

IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021-1. <https://www.iucnredlist.org>. (accessed 28 may 2021).

Lenoir, J.; Svenning, J.-C. Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, 38: 15-28. 2015.

MACHADO, M.; YOUNG, C.; CLAUZET, M. Environmental Funds to Support Protected Areas: Lessons From Brazilian Experiences. *PARKS. The International Journal of Protected Areas and Conservation*, Volume 26.1, Gland, Switzerland: IUCN
Anderson, R. P. 2017. When and how should biotic interactions be considered in models of species niches and distributions? *J. Biogeogr.*, 44: 8-17. 2020.

MAWDSLEY, J. R.; O'MALLEY, R.; OJIMA, S. O. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. **Conserv Biol** 23:1080–1089. 2009.

MMA. Portaria no 443, de 17 de dezembro de 2014. Diário Of. da União. 110-121.

PARMESAN, C; YOHE, G. A Globally Coherent Fingerprint Of Climate Change Impacts Across Natural Systems. **Nature**. 421. 2003. 2014.

PECL, G.; ARAÚJO, M.; BELL, J.; BLANCHARD, J.; BONEBRAKE, T.; CHEN, L.; et al. Biodiversity Redistribution Under Climate Change: Impacts on Ecosystems and Human Well-being. **Science**. 355 (6332). 2017.

PEREIRA, H., LEADLEY, P., PROENÇA, V., ALKEMADE, R., SCHARLEMANN, J., FERNANDEZ, J., ARAÚJO, M., BALVANERA, P., BIGGS, R., CHEUNG, W., CHINI, L., COOPER, H., GILMAN, E., GUENETTE, S., HURTT, G., HUNTINGTON, H., OBERDORFF, T., REVENGA, C., WALPOLE, M. Scenarios for Global Biodiversity in the 21st Century. **Science**. 330. 1496-1501. 2010.

SOBERÓN, J., PETERSON, A.. Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. **Biodiversity Informatics**. 2. 2005.

SVENNING, J., SKOV, F. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? **Ecology letters**. 10. 453-60. 10.1111/j.1461-0248.2007.01038.x. 2007.

TORRES, R.; MARENGO, J. Climate Change *Hotspots* Over South America: From CMIP3 to CMIP5 Multimodel Datasets. **Theor Appl Climatol**, 117, 579–587. 2014.

WRIGHT, K. B. Researching Internet-Based Populations: Advantages and Disadvantages of Online Survey Research, Online Questionnaire Authoring Software Packages, and Web Survey Services. **J. Computer-Mediated Communication**. 10. 10.1111/j.1083-6101.2005.tb00259.x. 2005.

ZWIENER, V. P. Climate Change as a Driver of Biotic Homogenization of Woody Plants in the Atlantic Forest. **Global Ecol Biogeogr**. v. 27. p. 298–309. 2018.

ZWIENER, V. P., PADIAL, A. A., MARQUES, M. C M., FALEIRO, V. F.; LOYOLA, R.; PETERSON, A. T. Planning for conservation and restoration under climate and land use change in the Brazilian Atlantic Forest. **Diversity and Distributions**. 23. 955-966. 2017.

The potential distribution of *Araucaria angustifolia* in the future will not be as reduced as thought, but its conservation demands urgent actions

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HIGHLIGHTS

- *Araucaria angustifolia* may respond to climate change with a reduction of 45% to 56% in its potential distribution.
- 52-74% of the potential distribution may no longer be within protected areas in 2050.
- Distribution areas within grassland will remain stable in future projections.

ABSTRACT

Araucaria angustifolia is a Critically Endangered pine tree of great ecological, economic and cultural importance. Using Ecological Niche Modeling we estimated its distribution in the present and future scenarios (2050), assessed sources of uncertainties, and evaluated the effectiveness of protected areas. For this, we generated and compared 11,484 models with different combinations of variables and parameters. The final model included variables related to climate, soil and topography. The potential distribution of *Araucaria* was estimated to be $489.8 \times 10^3 \text{ km}^2$, with a reduction in 2050 from 45% to 56% depending on the scenario (SSP2-4.5 and SSP5-8.5). When considering the reduction within remaining habitats, estimates ranged from 27% to 40%. Combined, current habitat availability and climate change constraints accounted for a reduction from 66% to 72% of the overall potential distribution. In addition, 52-74% of the potential distribution may no longer be within protected areas in 2050. We show that estimates of *A. angustifolia* distribution in the future are variable and dependent on climate projections and scenarios, however, the potential distribution in natural grasslands may remain stable. Coordinated actions

involving protection and restoration of habitats associated with population growth may improve the persistence of *Araucaria* in the future.

Keywords: Biodiversity conservation, Climate change, Ecological niche modeling, Model uncertainty.

INTRODUCTION

Climate change represents a major threat to biodiversity and human well-being, raising concern across the globe (Pereira et al, 2010; Zwiener et al., 2018). Critically Endangered species, which are more exposed to global changes, are of particular concern (IUCN, 2021). The emblematic conifer *Araucaria angustifolia* (Bertol.) Kuntze is a CR tree species that plays crucial ecological, economic and cultural roles. This species is highly threatened mainly because of overexploitation of its valuable timber and land-use changes, which have been directly or indirectly linked to timber exploitation (Carlucci et al., 2021). Recent studies suggest that climate change may lead to a reduction in the environmental suitability for the species within its current distribution range (Castro et al., 2019; Marchioro et al., 2020; Wilson et al., 2019; Wrege et al., 2017). For instance, Wilson et al. (2019) reports that the species would be restricted to highlands representing only 3.5% of its current distribution by 2070. Despite the important contribution of these studies to the understanding of distributional patterns of *A. angustifolia*, a comprehensive assessment of the effects of climate change and the implications for its conservation are still needed to guide management actions and public policies.

Araucaria is conifer tree that occurs in the Atlantic Forest. The species usually occurs in highlands, between 500 and 2300 m above sea level (Carvalho, 1994), but it is also found in natural populations at lower elevations in higher latitudes (up to 31.5° S), in the Pampa ecoregion (Hueck, 1953; Wrege et al., 2017). Its growth is affected by humidity, evapotranspiration, soil conditions, and competition within and between species (Brandes et al., 2021). This conifer is considered a keystone plant resource, because its seeds are an essential food resource for the fauna during the winter, when there is scarcity of fruits and seeds in the forest (Bogoni et al., 2020). Moreover, it is also a culturally important species, especially in southern Brazil, where its highly caloric seeds are widely traded and consumed by the human population (Tagliari et al., 2021). For such reasons, *Araucaria* is associated with several city and locality names and even celebrated on the state of Paraná coat of arms. The ecoregion characterized by the *Araucaria* – Araucaria Forest – has suffered a reduction of at least 87% of its distribution in the past decades due to deforestation (Carlucci et al., 2021; Ribeiro et al., 2009). Considering the importance of this species for ecosystem functioning and its contributions to people, it is paramount to understand whether its geographical distribution will remain suitable in the future in order to guide conservation efforts towards its long-term persistence. In this sense, Ecological Niche Modeling (ENM) may help unveil how future climate change will impact *Araucaria*'s distribution.

Protected areas (PAs) are the cornerstone of biodiversity conservation worldwide, and they are key for climate change adaptation and mitigation policies (Elsen et al., 2020; Mawdsley et al., 2009). PAs play an important role serving as stepping stones for species tracking suitable climates, may help buffer the

changes in environmental conditions, and can act as local climate refugia for resident species (Belote et al., 2017; Mawdsley et al., 2009). PA locations are fixed and, as climate changes, the effectiveness of a PA in maintaining suitable conditions for species persistence might be compromised, impairing its efficiency in ensuring species persistence in the long term (Hannah et al., 2007; Elsen et al., 2020). Therefore, it is paramount to evaluate the role of the PA system in safeguarding suitable conditions for threatened species facing climate change, as the iconic *Araucaria* itself. A critical judgement of their effectiveness under different climate change scenarios is decisive for guiding management actions and public policies (Machado et al., 2020; Zwiener et al., 2017)

Despite *Araucaria*'s cultural, economic and ecological importance, not until very recently its potential response to climate change has been explored (Bergamin et al., 2019; Castro et al., 2019; Marchioro et al., 2020; Wilson et al., 2019; Wrege et al., 2017), albeit with significant limitations. According to these studies, the current potential distribution ranges from 292,983 to 502,769 km², depending on variables, algorithms, and model settings. Moreover, estimates of climate change effects on *Araucaria*'s distribution go from potential range expansion to absolute extinction, with an overall reduction of PAs effectiveness in the future. However, ENM uncertainty has not been assessed and none of the previous studies have explicitly considered the accessible areas selected for model calibration. Equally varied are the predictor variables used for modeling, yet model performance with different combinations of settings and environmental predictors have not been compared (but see Marchioro et al., 2020). Another potential issue is that occurrences at the edge of the geographical distribution of *Araucaria* were not considered by most studies, e.g. areas in the southern edge

in the Pampa, which may bias the niche models and estimates of the future species distribution, these limitations likely blur inferences of species current distribution and potential response to climate change (Wisz et al., 2008; Peterson et al., 2011).

In this context, our study aimed to: (i) estimate the geographic distribution of *Araucaria* in the present and in future climate scenarios (2050); (ii) assess and present spatially explicit visualizations of model uncertainty; (iii) evaluate if PAs accommodate the potential distribution of *Araucaria* in the present and alternative future scenarios. We expect that the *Araucaria* distribution is mostly driven by precipitation, soil and topographic factors associated with microclimate. We also expect *Araucaria* to retract its distribution in general but maintain climatic stable areas in southern Brazil. Further, we expect that only a small percentage of the potential distribution is within PAs and that these areas will become even less effective in future scenarios.

METHODS

Occurrence data

The occurrence data was obtained from SpeciesLink (<http://www.splink.org.br/>), Brazilian virtual herbarium program REFLORA (<http://www.herbariovirtualreflora.jbrj.gov.br>), and GBIF (<https://www.gbif.org/>).

We started with total of 540 occurrence points, and after excluding duplicates and the ones that were wrong referenced, in the ocean, in the wrong biome, or regions that don't are pointed by specialists, the results were 294 useful points located in Brazil, Argentina and Paraguay. Additionally, we obtained 34 occurrence points from Ferrer (2019), located at the southernmost area of the species' known distribution, in southern Brazil (state of Rio Grande do Sul). These occurrence points add new and important information to the niche model. To reduce sampling bias, we used a distance filter (spatial thinning) to exclude nearby records according to categories of environmental heterogeneity. After data cleaning and thinning processes, we retained a total of 131 records for modeling (Appendix A). For independent evaluation of models, we obtained occurrences from forest inventories (Appendix B) across the Atlantic Forest. Despite sharing similar sampling biases, the spatial distribution of herbarium records and forest inventories are weakly correlated (Zwiener et al., 2021).

Environmental variables

Bioclimatic layers were obtained from WorldClim v2.1 (<https://worldclim.org/>; Fick and Hijmans, 2017) for present and future scenarios

(2050 CMIP6), considering two Shared Socioeconomic Pathways (SSPs) scenarios, SSP2-4.5 and SSP5-8.5, and four Global Circulation Models (GCMs): BCC-CSM2-MR, CanESM5, CNRM-ESM2-1, MIROC-ES2L. (See Appendix C for GCM selection criteria). The SSPs represents five different ways that the world will deal with the mitigation of climate change, with multiple baselines underlying factors, such as population, technology, economic growth, that could lead to very different future emissions and warming outcomes. We selected 2 different scenarios, SSP2-4.5 as a realistic scenario, with medium challenges to mitigation and adaptation, and SSP5-8.5 as a pessimistic, with the highest carbon emission, and without an action in climatic mitigations.

We also obtained raster layers of soil bulk density (bulk), weight percentage of sand particles (sand) and weight percentage of clay (clay) from SoilGrid (<https://soilgrids.org>). In addition, we generated an Aspect Index and a Topographic Wetness Index (TWI) from GTOPO 30, a global digital elevation model (DEM) with a horizontal grid spacing of 30 arc seconds (approximately 1 kilometer) (USGS). These variables were generated based on a digital elevation model in the SAGA GIS software (<http://www.saga-gis.org/>). After variable selection (Appendix D) we kept bio 1 (Annual Mean Temperature), bio 3 (Isothermality), bio 7 (Temperature Annual Range), bio 10 (Mean Temperature of Warmest Quarter), bio 12 (Annual Precipitation), bio 13 (Precipitation of Wettest Month), bio 17 (Precipitation of Driest Quarter), bulk, sand and TWI. All layers had their scales adjust to 2.5 arc-minutes resolution, by the resample tool in Rstudio, with the package Raster, that transfers values between non matching Raster.

Ecological niche modeling

The explicit consideration of accessible areas (**M**; Soberón and Peterson, 2005) is fundamental for the calibration of ecological niche models and their projections (Merow et al., 2013). This consideration allows for better estimations of potential areas of distribution of a species (Soberón, 2010). Here, we implemented a novel simulation approach to estimate **M**, which considers changing scenarios of environmental suitability, along with dispersal and colonization events and potential biogeographical barriers (Machado-Stredel et al. in review). We generated multiple simulations with different settings and environmental variables and all of them have good results on the validation simulation with fossil pollen records of *Araucaria* (Appendix E).

The objectives and data characteristics should guide the choice of algorithms, we opted to use Maxent (3.4.1) since, accordingly with studies, has the best performance in models without absence points (Qiao et al., 2015). Implemented in the *kuenm* package (Cobos et al., 2019a). Given distinct parameter settings, we tested candidate models resulting from all combinations of three feature classes (linear, quadratic and product), six regularization multipliers (0.1, 0.25, 0.5, 1, 2, 4), and 638 sets of environmental variables (in groups of 3 to 5 of the variables previously selected). Maxent allows fitting complex responses to environmental variation, we opted for a more conservative approach by selecting feature classes that are supported by ecological theory and are less prone to overfitting (Merow et al., 2013).

The models were trained with a set of 70% of randomly partitioned occurrences. The remaining 30% of the data was used to evaluate and select

models based on the following criteria: (i) statistical significance with partial ROC test (Peterson et al., 2008); (ii) omission rate (admitting $E = 5\%$ omission “error”); (iii) and the Akaike information criterion (AICc). For the background, 10050 points were used, and we choose to use the model created from free extrapolation. After selecting the model that met the significance and omission rate criteria, with the lowest AICc value, we generated a final model with the selected parameters, all occurrences, five Maxent bootstrap replicates, and projections to all future scenarios. This final model was evaluated with the independent dataset using the criteria of statistical significance and omission rates with a 5% threshold.

Continuous values of suitability were transformed into binary (1=suitable and 0=unsuitable) based on a corrected minimum presence value, assuming an omission error level of 5% (COBOS et al., 2019). The models and analyzes were developed in the computational environment R 4.0.3 (R Core Team 2018).

Spatial restriction and model uncertainty

We opted to constrain the projections of the final model based on the observation that some sites predicted suitable were distant from localities where *Araucaria* has been detected. To deal with the ENM potential overprediction, we used *a posteriori* presences-based restriction (PRES) to spatially delimit the current *Araucaria* distribution (Mendes et al., 2020). The PRES restriction was performed using the package MSDM (Mendes et al., 2020). To evaluate the impact of climate change on the *Araucaria* future distribution, we assumed a scenario of no dispersal, that is, the future projected distribution is spatially constrained to the current distribution range.

We assessed variability in the final models by quantifying and mapping the variance coming from Maxent replicates, SSPs, and GCMs (Cobos et al., 2019b). To assess risks of extrapolation derived from the presence of environmental conditions in future scenarios that are non-analogous to current conditions, we performed mobility-oriented parity analyses with 5% percentage of values sampled from the calibration region to calculate the MOP (MOP; Owens et al., 2013). All these analyses were performed using the package *kuenm*.

Additionally, we tested whether environmental suitability changes significantly across scenarios in the localities where the species has been detected. For each occurrence record, we extracted the suitability value of the Maxent logistic output for the present and future scenarios. A one-way analysis of variance (ANOVA) with permutation tests was used to compare suitability among scenarios. Pairwise differences were assessed using the Fisher's Least Significant Difference test (LSD) with Bonferroni's correction ($p < 0.05$). The ANOVA with permutation test and LSD analyses were performed with the packages *ImPerm* (Wheeler and Torchiano, 2016) and *agricolae* (Mendiburu, 2017), respectively.

Habitat remnants and protected areas

We used spatially explicit data on areas identified as urban, cropland, pasture, native forest and grasslands for 2019 obtained from MapBiomass (<https://mapbiomas.org/>; Souza et al., 2020). With this layer, we identified and quantified areas of the different land uses within the areas of potential distribution

for the species. The spatial layer of protected areas was obtained from the World Conservation Monitoring Center (UNEP-WCMC) and IUCN (2020) database.

RESULTS

A total of 11,484 candidate models were generated and compared, with one model meeting the criteria of significance, prediction and parsimony. The selected model was ranked sixth lowest AICc, however it was the single model reaching an omission error smaller than 0.05. The model was fit with regularization multiplier 0.1, linear and quadratic feature classes and the variables bio 3, bio 7, bio 12, bulk, TWI. Model averaging indicated bulk, bio 7 and bio 13 as the overall three most important variables across all models, two out of which were included in the final model. The validation of the final model with independent data corroborated the statistical significance and resulted in an omission rate of zero (Appendix E).

The potential geographic distribution of *Araucaria* covered an area of 489.8 x10³ km², distributed in the south and southeast of Brazil, and scattered in small portions in Argentina and Paraguay near the border with Brazil. This potential distribution has been, however, restricted by habitat reduction. Nearly 45% of the total estimated distribution area contain remnants of native forests, and 2% of native grasslands, which together account for 47% of remaining natural habitat where populations of *Araucaria* are projected to occur (Table 1 and Figure 1).

In both future scenarios (SSP2-4.5 and SSP5-8.5), our projections revealed a significant reduction of the potential distribution of *Araucaria* by 2050,

based on the consensus of GCMs. Overall, climate change may contribute similarly (45-56%) to the reduction of distribution, when compared to the impacts of land-use change to the current distribution (53%). Both drivers of global changes restricted potential suitable sites to only 34% under scenario SSP2-4.5 and 28% under SSP5-8.5 (Table 1). Area reductions are predicted mostly in western and northern portion of the current distribution. Regarding *Araucaria* conservation, 16% of the current potential distribution fall within PAs, and only 11% contain remnants of natural vegetation. However, PAs with remaining habitat covered merely 5% of the potential distribution under scenario SSP2-4.5 and 4% under SSP5-8.5 (Figure 1).

Among the sources of ENM uncertainty assessed here, variance from GCMs represented the largest source, followed by replicates and emission scenarios (Figure 2). The uncertainty was not evenly distributed across the region, with GCM variance mostly concentrated at the limits of distribution near the coast, and northeastern and western sites. Projections to the different GCMs showed reduction of *Araucaria*'s distribution under scenario SSP2-4.5 and more intensively under scenario SSP5-8.5 in 2050. The areas that represent extrapolation risk in future projections do not affect where the model indicates the presence of the species (appendix F).

Overall, the environmental suitability at the localities of remaining *Araucaria* populations, represented by occurrence points, significantly reduced in future scenarios (ANOVA, $p < 0.05$). On average, the reduction was higher in scenario SSP5-8.5 than SSP2-4.5, however, the variation was highly variable across GCMs (Figure 3).

DISCUSSION

Our results show that *Araucaria* may respond to climate change with a reduction of 45% to 56% in its potential distribution. If considered the distribution within the remaining habitat (47%), the reduction is estimated to 27-40%, which suggests that some sites deemed unsuitable in the future are in already impacted and deforested landscapes. Further, we show that projections of *Araucaria* distribution in the future are variable and dependent on GCMs and scenarios under consideration (Appendix G). PAs cover a small proportion of *Araucaria*'s potential distribution and may become even less effective in the future, highlighting the need for protection and restoration actions to safeguard such an important species.

The geographic distribution of *Araucaria* has been the focus of recent studies assessing its response to future climate change and evaluating the effectiveness of PAs (Castro et al., 2019; Marchioro et al., 2020; Wilson et al., 2019). To obtain precise estimates within the ENM framework, it is essential to understand the ecological factors and species' characteristics that drive geographic distributions (Peterson et al., 2011). We opted for an exploratory approach by including as predictor variables known climatic factors that influence the distribution of *Araucaria* and modulate its growth, such as annual precipitation and temperature variation (Brandes et al., 2021) and other variables that had not been previously assessed, but may also have an important role, for instance, soil bulk density. In fact, *Araucaria* performs better in soils rich in organic matter, nutrients, and biological activity, which make the soil denser (Hoogh and Dietrich,

1979). Additionally, we found evidence for effects of microclimate linked to topography and water accumulation in the landscape, which are important factors also suggested by Wilson et al. (2019). Thus, modeling the ecological niche of *Araucaria* based solely on climatic variables is likely to generate inaccurate estimates, which may be aggravated if potential distributions are projected to future scenarios (Coudun et al., 2006)

In addition to environmental factors, human activity has also influenced the geographic distribution of *Araucaria*, leading to range expansion and contraction (Behling et al., 2002; Brandes et al., 2021; Lauterjung et al., 2018). Groups of pre-Columbian humans played an important role dispersing the seeds of *Araucaria*, potentially increasing its area of distribution in the past (Lauterjung et al., 2018; Robinson et al., 2018). However, in the 20th century, due to the intensive timber extraction, overexploitation of seeds and land-use changes, populations of *Araucaria* have been drastically reduced, leading the species to the status of Critically Endangered (Carlucci et al., 2021). Despite being an Endangered species, in which cutting is prohibited by law loggings by fraudulent bidding processes still occur, particularly in the Brazilian states of Santa Catarina and Paraná (Brandes et al., 2020). Contractions are predicted mostly in the northern and western portion of the distribution, however, with significant variation across scenarios and climate projections. Our predictions differ from those obtained by Wilson et al. (2019) demonstrating a less drastic scenario and shed light into the potential variability of future projections. Most importantly, we highlight the negative effects of anthropogenic impacts such as land-use and climate change that may act in synergy and further imperil remaining *Araucaria* populations in the near future.

In this scenario PAs and forest management strategies are central in providing conditions for the species reproduction and survival. There are few PAs that guarantee the protection of the *Araucaria* Forest, only 334 (SSP2-4.5) - 245 (SSP5-8.5) according to our projections, and our models show that more than 52-74% of *Araucaria*'s potential distribution may no longer be within current PAs by 2050. Therefore, new protection measures must be considered. A first step to be taken is to protect large climatically-stable remnants not covered yet by PAs. Moreover, our results demonstrate that large tracts of areas with grassland will remain stable in future projections. Therefore, the historical expansion of *Araucaria* Forests over grasslands (Behling et al., 2002) could continue depending on local management (see Oliveira and Pillar 2004; Sühs et al., 2018). Besides the creation of public PAs, voluntary strategies of conservation in private lands (Kamal et al., 2015), as the creation of private PAs and the Payment for Environmental Services, should be encouraged to stimulate landowners to protect *Araucaria* and the associated ecosystems beyond legal obligation. In degraded lands, restoration actions could increase connectivity, guarantee genetic flow, and promote greater chances of survival for populations of *Araucaria* (Stefenon et al., 2007) in future climatic scenarios. Coordinated actions involving protection and restoration of habitats associated with population growth may improve the persistence of *Araucaria* in the future.

Our results were based on important factors that influence ENM output that were not previously considered: particularly, the inclusion of occurrences across the entire geographical range of the species, estimation of accessible areas, selection and comparison of multiple variables and model settings. We show that climate change represents a major threat to *Araucaria*, however, such estimates

are variable and dependent on scenarios and climate projections. In line with previous studies, we stress that the current PAs network is insufficient to safeguard *Araucaria* in face of climate change and urgent actions need to be implemented for its long-term persistence.

CONFLICTS OF INTEREST

None declared.

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REFERENCES

- Behling, H. 2002. South and Southeast Brazilian Grasslands during Late Quaternary times: a synthesis. *Palaeogeography* 177, 19-27, [https://doi.org/10.1016/S0031-0182\(01\)00349-2](https://doi.org/10.1016/S0031-0182(01)00349-2).
- Belote, R.T., Dietz, M.S., Jenkins, C.N., McKinley, P.S., Irwin, G.H., Fullman, T.J., Leppi, J.C., Aplet, H.A. 2017. Wild, connected, and diverse: Building a more resilient system of protected areas. *Ecol Appl* 27, 1050–1056. <https://doi.org/10.1002/eap.1527>.
- Bergamin, R.S., Debastiani, V., Joner, D.C., Lemes, P., Guimarães, T., Loyola, R.D., Müller, S.C. 2019. Loss of suitable climatic areas for *Araucaria* forests over time. *Plant Ecology & Diversity* 12(2), 115-126, <https://doi.org/10.1080/17550874.2019.1618408>.
- Bogoni, J.A., Muniz-Tagliari, M.M., Peroni, N., Peres, C.A. 2020. Testing the keystone plant resource role of a flagship subtropical tree species (*Araucaria angustifolia*) in the Brazilian Atlantic Forest. *Ecological Indicators* 118, 106778. ISSN 1470-160X, <https://doi.org/10.1016/j.ecolind.2020.106778>.
- Brandes, A.F.N., Albuquerque, R.P., Lisi, C.S., Lemos, D.N., Nicola, L.R.M., Barros, C.F. 2021. The growth responses of *Araucaria angustifolia* to climate are adjusted both spatially and temporally at its northern distribution limit. *Forest Ecology and Management* 487, <https://doi.org/10.1016/j.foreco.119024>.

Brandes, A.F.N., Novello, B.Q.N., Domingues, G.A.F., Barros, C.F., Tamaio, N. 2020.

Endangered species account for 10% of Brazil's documented timber trade.

Journal for Nature Conservation 55, <https://doi.org/10.1016/j.jnc.2020.125821>.

Brown, J.L., Bennett, J., French, C.M. 2017. SDMtoolbox: the next generation

python-based GIS toolkit for landscape genetic, biogeographic and species

distribution model analyses. PeerJ 5(5), 4095,

<https://doi.org/10.7717/peerj.4095>.

Carlucci, M.B., Marcilio-Silva, V., Torezan, J.M.D. 2021. The Southern Atlantic

Forest: Use, Degradation, and Perspectives for Conservation. In: Marques

M.C.M., Grelle C.E.V. (eds) The Atlantic Forest. Springer, Cham.

https://doi.org/10.1007/978-3-030-55322-7_5

Carvalho, P. 1994. Espécies florestais brasileiras: recomendações silviculturais,

potencialidades e usos da madeira. Colombo: EMBRAPA/CNPQ. 640.

Castro, M.B., Barbosa, A.C., Pompeu, P.V., Eisenlohr, P.V., Pereira, G.A.,

Guimarães, D.M., Pires-Oliveira, J.C., Barbosa, J.P.R.A.D., Fontes, M.A.L.,

Santos, R.M.S., Phin, D.Y. 2019. Will the emblematic southern conifer

Araucaria angustifolia survive to climate change in Brazil? Biodivers Conserv.

29, 591–607, <https://doi.org/10.1007/s10531-019-01900-x>.

Cobos, M.E., Peterson, A.T., Barve, N., Osorio-Olvera, L. 2019b. kuenm: An R

package for detailed development of ecological niche models using Maxent.

PeerJ 7 e6281, <https://doi.org/10.7717/peerj.6281>.

Cobos, M.E., Peterson, A.T., Osorio-Olvera, L., Jiménez-García, D. 2019c. An

exhaustive analysis of heuristic methods for variable selection in ecological

niche modeling and species distribution modeling. *Ecological Informatics* 53.
<https://doi.org/10.1016/j.ecoinf.2019.100983>.

Coudun, C., Gégout, J., Piedallu, C., Rameau, J. (2006). Soil nutritional factors improve models of plant species distribution: An illustration with *Acer campestre* (L.) in France. *Journal of Biogeography*. 33. 1750 - 1763.
<https://doi.org/10.1111/j.1365-2699.2005.01443.x>.

Duarte, L.D.S., Dos-Santos, M.M.G., Hartz, S.M., Pillar, V.D. 2006. Role of nurse plants in *Araucaria* Forest expansion over grassland in south Brazil. *Austral Ecology* 31, 520-528. <https://doi.org/10.1111/j.1442-9993.2006.01602.x>.

Elsen, P.R., Monahan, W.B., Dougherty, E.R., Merenlender, A.M. 2020. Keeping pace with climate change in global terrestrial protected areas. *Sci Adv* 6,
<https://doi.org/10.1126/sciadv.aay0814>.

Ferrer, R.S. 2019. Florestas mistas de coníferas na província biogeográfica do Pampa: variações estruturais dos enclaves de coníferas mais austrais do Brasil. Tese de Doutorado, Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul.

Fick, S., Hijmans, R. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302-4315, <https://doi.org/10.1002/joc.5086>.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R. and Williams, P. 2007. Protected area needs in a changing climate. *Frontiers in Ecology and the Environment* 5, 131-138,
<https://doi.org/10.1890/1540-9295>.

Hoogh, R., Dietrich, A. 1979. Avaliação de sítio para *Araucaria angustifolia* (Bert.)O. Kuntze. em povoamentos artificiais. *Ciência Florestal* 17(3), 247-256.

Hueck, K. 1953. Distribuição e habitat natural do pinheiro do paran  (Araucaria angustifolia). *Boletim da Faculdade de Filosofia, Ci ncias e Letras, Universidade de S o Paulo. Bot nica* 10, 5-24,
<https://doi.org/10.4336/2017.pfb.37.91.1413>.

IUCN. 2021. The IUCN Red List of Threatened Species. Version 2021-1.
<https://www.iucnredlist.org>. (accessed 28 may 2021).

Kamal, S., Grodzi ska-Jurczak, M., Brown, G. 2015. Conservation on private land: a review of global strategies with a proposed classification system. *Journal of Environmental Planning and Management*, 58(4), 576-597.
<https://doi.org/10.1080/09640568.2013.875463>

Lauterjung, M.B. , Bernardi, A., Montagna, T., Ribeiro, R., Costa, N., Mantovani, A., Reis, M. 2018. Phylogeography of Brazilian pine (*Araucaria angustifolia*): integrative evidence for pre-Columbian anthropogenic dispersal. *Tree Genetics & Genomes*. 14 (3), <https://doi.org/10.1007/s11295-018-1250-4>.

Machado, M., Young, C., Clauzet, M. 2020. Environmental Funds to Support Protected Areas: Lessons From Brazilian Experiences. *PARKS. The International Journal of Protected Areas and Conservation* 26 (1), IUCN.

Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M.G., Fieldand, C.B., Knowlton, N. 2020. Climate change and ecosystems: threats,opportunities and solutions.*Phil. Trans. R. Soc.* 375, <https://doi.org/10.1098/rstb.2019.0104>.

- Marchioro, C.A., Santos, K.L., Siminski, A. 2020. Present and future of the critically endangered *Araucaria angustifolia* due to climate change and habitat loss, *Forestry: An International Journal of Forest Research* 93(3), 401–410, <https://doi.org/10.1093/forestry/cpz066>.
- Mawdsley, J.R., O'Malley, R., Ojima, S.O. 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conserv Biol* 23, 1080–1089. <https://doi.org/10.1111/j.1523-1739.2009.01264.x>
- Mendes, P., Velazco, S.J.E., Andrade, A.F.A., De Marco, P.M. 2020. Dealing with overprediction in species distribution models: How adding distance constraints can improve model accuracy. *Ecological Modelling* 431. <https://doi.org/10.1016/j.ecolmodel.2020.109180>
- Mendiburu, F. (2010). *Agricolae: Statistical Procedures for Agricultural Research*. R package version. 1. 1-8. <http://CRAN.R-project.org/package=agricolae>.
- Merow, C., Smith, M.J., Silander, J.A. 2013. A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography* 36, 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>.
- Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G. 2014. Where is positional uncertainty a problem for species distribution modelling? *Ecography* 37, 191-203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>.
- Oliveira, J. M., Pillar, V. D. 2004. Vegetation dynamics on mosaics of Campos and *Araucaria* forest between 1974 and 1999 in Southern Brazil. *Community ecology*, 5(2), 197-202. <https://doi.org/10.1556/ComEc.5.2004.2.8>.

- Owens, H.L., Campbell, L.P., Dornak, L.L., Saupe, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E., Peterson, A.T. 2013. Constraints on Interpretation of Ecological Niche Models by Limited Environmental Ranges on Calibration Areas. *Ecological Modelling* 263, 10–18. <https://doi.org/10.1016/j.ecolmodel.2013.04.011>.
- Pereira, H., Leadley, P., Proença, V., Alkemade, R., Scharlemann, J., Fernandez, J., Araújo, M., Balvanera, P., Biggs, R., Cheung, W., Chini, L., Cooper, H., Gilman, E., Guenette, S., Hurtt, G., Huntington, H., Oberdorff, T., Revenga, C., Walpole, M. 2010. Scenarios for Global Biodiversity in the 21st Century. *Science* 330, 1496-1501. <https://doi.org/10.1126/science.1196624>.
- Peterson, A.T., Papeş, M., Soberón, J. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213, 63-72, <https://doi.org/10.1016/j.ecolmodel.2007.11.008>.
- Peterson, A.T., Soberón, J., Pearson, R., Anderson, R., Martínez-Meyer, E., Nakamura, M., Araújo, M. 2011. Ecological Niches and Geographic Distributions.
- Phillips, J., Anderson, P., Schapire, R. 2006. Maximum entropy modeling of species geographic distributions, *Ecological Modelling* 190, 231-259, <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Qiao, H., Soberón, J., Peterson, A. 2015. No silver bullets in correlative ecological niche modeling: Insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution* 6, 1126– 1136, <https://doi.org/10.1111/2041-210X.12397>

- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142 (6), 1141-1153, <https://doi.org/10.1016/j.biocon.2009.02.021>.
- Robinson, M., De Souza, J.G., Maezumi, S.Y. et al. 2018. Uncoupling human and climate drivers of late Holocene vegetation change in southern Brazil. *Sci Rep* 8, 7800, <https://doi.org/10.1038/s41598-018-24429-5>.
- Sühs, R. B., Giehl, E. L. H., Peroni, N. 2018. Interaction of land management and araucaria trees in the maintenance of landscape diversity in the highlands of southern Brazil. *PloS one*, 13(11), <https://doi.org/10.1371/journal.pone.0206805>.
- Soberón, J. 2010. Niche and area of distribution modeling: A population ecology perspective. *Ecography* 33 (1), 159–167. <http://doi.org/10.1111/j.1600-0587.2009.06074.x>.
- Soberón, J., Peterson, A. 2005. Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. *Biodiversity Informatics* 2, 1-10. <http://doi.org/10.17161/bi.v2i0.4>.
- Sørensen, R., Zinko, U., Seibert, J. 2006. On the Calculation of the Topographic Wetness Index: Evaluation of Different Methods Based on Field Observations. *Hydrology and Earth System Sciences* 10, 101-112, <https://doi.org/10.5194/hess-10-101-2006>.
- Souza, C., Zanin, S.J., Rosa, M., Parente, L., Alencar, A., Rudorff, B., Hasenack, H., Matsumoto, M., Ferreira, L., Souza-Filho, P., Oliveira, S., Rocha, W., Fonseca,

A., Balzani, C., Diniz, C., Costa, D., Monteiro, D., Rosa, E., Vélez-Martin, E., Azevedo, T. 2020. Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. *Remote Sensing* 12 (17), <https://doi.org/10.3390/rs12172735>.

Stefenon, V. M., Gailing, O., Finkeldey, R. 2007. Genetic structure of *Araucaria angustifolia* (Araucariaceae) populations in Brazil: implications for the in situ conservation of genetic resources. *Plant Biology*, 9(4), 516-525. <https://doi.org/10.1055/s-2007-964974>.

Tagliari, M.M., Levis, C., Flores, B.M., Blanco, G.D., Freitas, C.T., Bogoni, J.A., Vieilledent, G., Peroni, N. 2021. Collaborative management as a way to enhance *Araucaria* Forest resilience. *Perspectives in Ecology and Conservation*, 19 (2), 131-142, <https://doi.org/10.1016/j.pecon.2021.03.002>.

USGS. Global 30 Arc-Second Elevation (GTOPO30) Digital Object Identifier. <https://doi.org/10.5066/F7DF6PQS>

Varela, S., Anderson, R.P., García-Valdés, R., Fernández-González, F. 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. *Ecography* 37, 1084-1091. <https://doi.org/10.1111/j.1600-0587.2013.00441.x>.

Wheeler, B., Torchiano, M. 2016. ImPerm: Permutation Tests for Linear Models. R package version 2.1.0. <https://CRAN.R-project.org/package=ImPerm>.

Wilson, O.J., Walters, R.J., Mayle, F.E., Lingner, D.V., Vibrans, A.C. 2019. Cold spot microrefugia hold the key to survival for Brazil's Critically Endangered *Araucaria* tree. *Glob Change Biol.* 25, 4339– 4351. <https://doi.org/10.1111/gcb.14755>.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A. 2008.

Effects of sample size on the performance of species distribution models.

Diversity and Distributions 14, 763-773. [https://doi.org/10.1111/j.1472-](https://doi.org/10.1111/j.1472-4642.2008.00482.x)

4642.2008.00482.x

Wrege, M.S., Fritzens, E., Soares, M.T.S., Bognola, I.A., Sousa, V.A. de, Sousa, L.P.

de, Gomes, J.B.V., Aguiar, A.V. de, Gomes, G.C., Matos, M. de F.S., Scarante,

A.G., Ferrer, R.S. 2017. Distribuição natural e habitat da araucária frente às

mudanças climáticas globais. Pesquisa Florestal Brasileira. 37, 331–

346. <https://doi.org/10.4336/2017.pfb.37.91.1413>.

Zwiener, V.P., Lima, R.A.F., Sánchez-Tapia, A., Rocha, D.S.B., Marques, M.C.M.

2021. Tree diversity in the Brazilian Atlantic Forest: biases and general patterns

using different sources of information. In: Marques, M.C.M., Grelle C.E.V. (eds)

The Atlantic Forest. Springer, Cham. [https://doi.org/10.1007/978-3-030-55322-](https://doi.org/10.1007/978-3-030-55322-7_6)

7_6

.Zwiener, V.P., Lira-Noriega, A., Grady, C.J., Padial, A.A., Vitule, J.R.S. 2018.

Climate change as a driver of biotic homogenization of woody plants in the

Atlantic Forest. Global Ecol Biogeogr. 27, 298– 309.

<https://doi.org/10.1111/geb.12695>.

Zwiener, V.P., Padial, A.A., Marques, M.C.M., Faleiro, V.F., Loyola, R., Peterson,

A.T. 2017. Planning for conservation and restoration under climate and land use

change in the Brazilian Atlantic Forest. Diversity and Distributions 23, 955–966.

<https://doi.org/10.1111/ddi.12588>.

TABLES

Table 1 Potential distribution of *Araucaria angustifolia*, in Km² (x10³) and within remaining habitat and protected areas (PAs). Percentages in parentheses are in comparison to the total estimated distribution. Estimates are presented for the present and under two different emission scenarios (SSP2-4.5 and SSP5-8.5) in 2050.

Potential distribution	Present	SPP2-4.5	SPP5-8.5
Total	489.79 (100%)	271.52 (55%)	216.90 (44%)
Forest remnants	218.59 (45%)	157.15 (32%)	125.57 (26%)
Grasslands	33.75 (7%)	32.52 (6.6%)	32.12 (6.5%)
Grasslands + Forest remnants	230.65 (47%)	169.20 (34%)	137.62 (28%)
PAs	76.77 (16%)	36.58 (7%)	20.34 (4%)
Grasslands + Forest remnants + PAs	52.37 (11%)	26.11 (5%)	18.60 (4%)

FIGURES

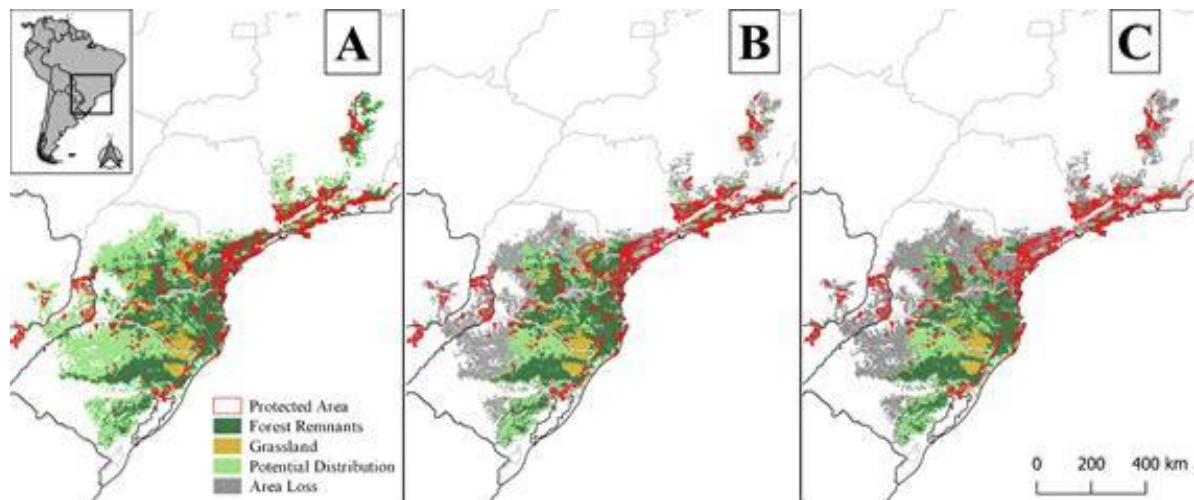


Figure 1. Potential distribution of *Araucaria angustifolia* within remnant habitat (forest and grasslands) and in protected areas. The estimates are shown in the present (A), under future scenarios SSP2-4.5 (B), and SSP5-8.5 (C) for 2050. Future distributions are represented by the consensus of projections on four Global Circulation Models. Note that the remaining habitat is presented only within the potential distribution.

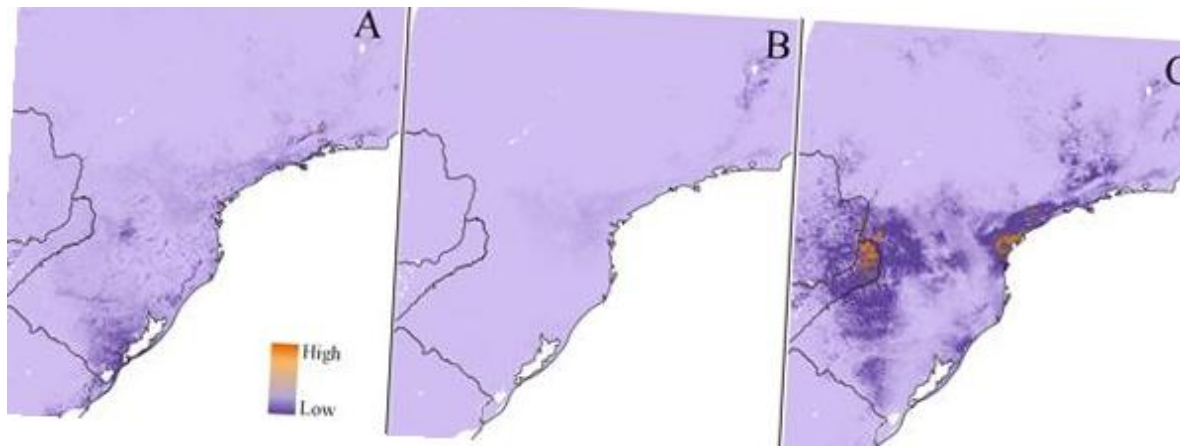


Figure 2. Geographical visualization of model sources of variance: (A) replicates; (B) emission scenarios (SSP2-4.5 and SSP5-8.5); (C) Global Circulation Models (BCC-CSM2-MR, CanESM5, CNRM-ESM2-1, MIROC-ES2L). The higher the value, more are the difference between the agreement of all layers of a category of variance.

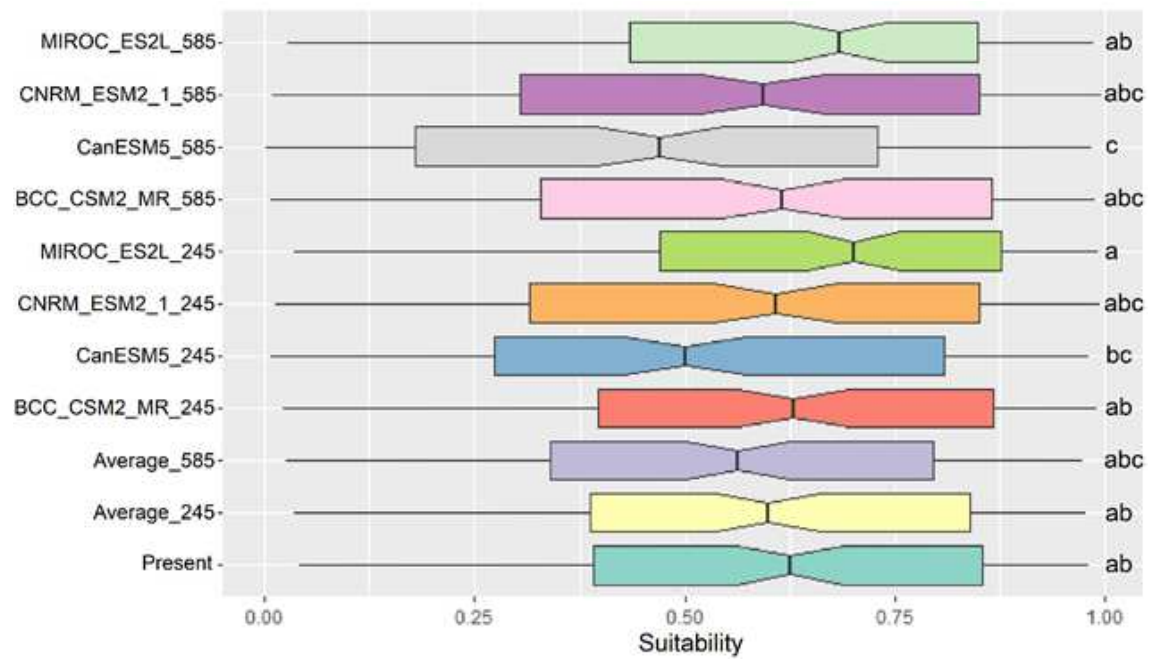


Figure 3. Variation of environmental suitability at the occurrence localities and across scenarios and GCMs. GCMs projections to scenario SSP5-8.5 have the suffix '_858', whereas projections to scenario SSP2-4.5 are marked by '_245'. Significant pairwise comparisons are represented by different letters on the right corner of the plot.

SUPPORTING INFORMATION

APPENDIX A. OCCURRENCE POINTS, DATA CLEANING AND THINNING

We obtained 540 occurrence points from SpeciesLink (<http://www.splink.org.br/>), Brazilian virtual herbarium program REFLORE (<http://www.herbariovirtualreflora.jbrj.gov.br>) and GBIF (<https://www.gbif.org/>). After initial steps of data cleaning (excluding duplicates, records that lacked coordinate precision, and georeferencing errors, opting for coordinates with more than 2 decimal number), we ended up with 328 useful points. Additionally, we obtained 34 occurrence points from Ferrer (2019), totaling 362 records.

Occurrence data is frequently obtained unsystematically, thus, many factors, such as detectability and proximity to human infrastructures, may lead to spatial variation in the presence and intensity of sampling (Varela et al., 2014; Zwiener et al., 2021). Based on the environmental variables used to calibrate our models, we obtained a layer of heterogeneity using an algorithm implemented in SDMTToolBox 2.0 (Brown et al., 2017). We classified this heterogeneity layer into three categories of decreasing heterogeneity, then the distances of 10km, 20km and 30km were applied to filter out nearby occurrences that were in the respective categories.

Occurrence points of *araucaria angustifolia* used in the niche modeling

Longitude	Latitude
-53.1576	-25.2072
-51.6953	-25.4212
-51.2406	-27.8269
-51.1425	-27.4936
-51.0167	-26.7833
-50.683	-26.9167
-50.5853	-27.2833
-50.3904	-26.1811
-52.4425	-31.2328
-52.9117	-31.3453
-53.2747	-31.1047
-52.7072	-30.645
-53.4839	-30.5569
-53.0344	-30.7697
-52.1725	-30.6267
-51.9172	-30.8378
-52.4278	-30.0172
-52.7964	-30.9669
-52.8078	-30.0581
-54.3943	-25.4035
-53.7801	-25.2397
-53.5391	-26.9833
-53.0658	-26.8758
-52.8167	-25.4667
-52.7097	-27.3939
-52.7	-30.5
-52.3325	-30.335
-51.6942	-24.2801
-51.4006	-26.5461
-51.3986	-25.325
-51.3883	-26.9072
-51.2247	-27.4017
-50.8497	-28.035
-50.6515	-25.4711
-50.35	-27.7833
-50.3226	-26.1106
-50.3084	-24.1431
-49.564	-27.2474
-49.1181	-27.0069
-44.1011	-21.4842
-42.8681	-20.7614
-52.35	-31.2472
-52.3683	-31.4658
-53.3511	-30.45
-53.3814	-30.2569
-52.5097	-30.5897
-52.5953	-31.5569

-52.8669	-31.7433
-54.0999	-26.6301
-53.9872	-26.5188
-53.7667	-26.0333
-53.6597	-25.0717
-53.4206	-24.9372
-53.2514	-24.5614
-52.95	-25.55
-52.7951	-26.4284
-52.7847	-27.1078
-52.3608	-24.0486
-52.31	-24.2061
-51.9914	-26.4883
-51.99	-26.8217
-51.8451	-25.9452
-51.6625	-27.0747
-51.5726	-25.0699
-51.5678	-27.3611
-51.2495	-29.2762
-51.2403	-26.3247
-51.2159	-23.3257
-50.9356	-29.0014
-50.7385	-29.2764
-50.67	-28.2603
-50.5756	-29.4206
-50.5517	-28.3481
-50.4167	-24.5167
-50.4	-29.4167
-50.2569	-24.6528
-50.1744	-29.4808
-50.1275	-27.9275
-50.0766	-29.1615
-50.0739	-27.5539
-50.0261	-25.6033
-49.9986	-25.4197
-49.9729	-25.1853
-49.9478	-28.4389
-49.9341	-27.9514
-49.9167	-28.3
-49.8221	-28.0252
-49.7692	-28.2606
-49.6861	-26.3675
-49.6536	-25.4689
-49.5911	-28.0825
-49.5123	-26.4321
-49.4919	-28.0131
-49.4898	-27.8011
-49.4595	-25.4689
-49.4108	-27.6292
-49.3889	-26.2939

-49.3726	-26.5595
-49.3689	-25.4269
-49.3336	-27.7003
-49.2671	-25.429
-49.1995	-25.9322
-49.1678	-25.3228
-49.1149	-25.4019
-48.6789	-24.5575
-47.0722	-23.7245
-46.9714	-23.7041
-46.7738	-23.6625
-46.7414	-23.5631
-46.6628	-22.6867
-46.6184	-23.6461
-46.3556	-22.0956
-46.0397	-22.8683
-45.5903	-22.7339
-45.3197	-22.5819
-45.31	-23.2217
-45.1058	-22.4583
-44.9994	-21.2453
-44.9389	-22.4206
-44.7389	-22.2372
-44.6292	-22.3691
-44.6033	-21.9761
-44.5634	-22.5
-44.2333	-22.4333
-43.9219	-21.7147
-43.7313	-22.1411
-43.5	-20.1333
-43.4936	-20.8389
-43.3725	-21.7302
-43.0499	-22.3379

APPENDIX B – REFERENCE OF THE VALIDATION POINTS

- Carmo, M. R. & Assis, M. (2012). Structural and floral characterization of the naturally fragmented forests in the Parque Estadual do Guartelá, Tibagy municipality, Paraná, Brazil. *Acta Botanica Brasilica*. 26. 133-145.
- Carvalho W. A. C., Filho, A. T. O., Fontes, M. A. L., Curi, N. (2007). Variação espacial da estrutura da comunidade arbórea de um fragmento de floresta semidecídua em Piedade do Rio Grande, MG, Brasil. *Revista Brasil. Bot.*, V.30, n.2, p.315-335, abr.-jun. 2007
- Catharino, E., Bernacci, L., Franco, G.A.D.C., Durigan, G., Metzger, J. (2006). Aspectos da composição e diversidade do componente arbóreo das florestas da Reserva Florestal do Morro Grande, Cotia, SP. *Biota Neotropica*. 6.
- Cordeiro, J., Rodrigues, W. Caracterização Fitossociológica de um Remanescente de Floresta Ombrófila Mista em Guuarapuava, PR. *Revista Árvore*, v.31(03). Sociedade de Investigações Florestais, Viçosa, p. 545-554.
- Cordeiro, J., Zwiener, V. P., Curcio, G. R., Roderjan, C. V. (2020). Edaphic Drivers of Community Structure and Composition in a Mixed Ombrophilous Forest. *FLORAM*, vol.27, n2.
- Silva, A., Higuchi, P. Negrini, M., Grudtner, A., Zech, D. (2013). Caracterização fitossociológica e fitogeográfica de um trecho de floresta ciliar em Alfredo Wagner, SC, como subsídio para restauração ecológica. *Ciência Florestal*. 23. 579-593.
- Carvalho, D., Vieira, A., Nakajima, J., Antonio, P., Carneiro, L. (1998). Composição florística e fitossociologia do componente arbóreo das florestas ciliares do rio Iapó, na bacia do rio Tibagi, Tibagi, PR. *Revista Brasileira de Botânica*.
- Floss, P. A. (2011). Aspectos Ecológicos e Fitossociológicos no Entorno de Nascentes em Formações Florestais do Oeste de Santa Catarina. (Tese de Doutorado). da Universidade Federal de Santa Maria (UFSM, RS) da Universidade Federal de Santa Maria (UFSM, RS).
- Fonseca, C. R. & Carvalho, F. A. (2012). Floristic and Phytosociological Aspects of the Tree Community in an Urban Atlantic Forest Fragment (Juiz De Fora, State Of Minas Gerais, Brazil). *Biosci. J.*, Uberlândia, v. 28, n. 5, p. 820-832, Sept./Oct.
- Giongo, C. & Waechter, J. L. (2007). Composição florística e espectro de dispersão das espécies arbóreas de uma floresta mista com *Podocarpus*, Rio Grande do Sul. *Revista Brasileira de Biociências*, Porto Alegre, v. 5, supl. 2, p. 333-335, jul.

- Gris, D. (2012). Riqueza e similaridade da vegetação arbórea do Corredor de Biodiversidade Santa Maria, PR. Riqueza e similaridade da vegetação arbórea do Corredor de Biodiversidade Santa Maria, PR. Dissertação (Mestrado) – Universidade Estadual do Oeste do Paraná.
- Guidini, A. L., Silva, A. C., Higuchi, P., Rosa, A. D., Spiazzi, F. R., Negrini, M., Ferreira, T. S., Salami, B., Marcon, A. K., Junio, F. B. (2014). Invasão por Espécies Arbóreas Exóticas em Remanescentes Florestais no Planalto Sul Catarinense. *Revista Árvore*, Viçosa-MG, v.38, n.3, p.469-478, 2014.
- Iurk, M. C., Santos, E. P., Dlugosz, F. L., Tardivo, R. C. Levantamento Florístico de Um Fragmento de Floresta Ombrófila Mista Aluvial do Rio Iguaçu, Município de Palmeira (PR). (2009). *Floresta*, Curitiba, PR, v. 39, n. 3, p. 605-617.
- Klauber, C., Paludo, G. F., Bortoluzzi, R. L. C., Mantovani, A. (2010). Florística e estrutura de um fragmento de Floresta Ombrófila Mista no Planalto Catarinense. *Biotemas*, 23 (1): 35-47.
- Leyser., G. Viniski, M., Donida, A. L., Zanin, E. M., Budke, J. C. (2009). Espectro de Dispersão em um Fragmento de Transição entre Floresta Ombrófila Mista e Floresta Estacional na Região do Alto Uruguai, Rio Grande do Sul, Brasil. *Pesquisas, Botânica* Nº 60:355-366 São Leopoldo: Instituto Anchieta de Pesquisas, 2009.
- Loures, L., Carvalho, D. A., Machado, E. L. M., Sá, J. J. G., Marques, M. (2007). Florística, estrutura e características do solo de um fragmento de floresta paludosa no sudeste do Brasil. *Acta bot. bras.* 21(4): 885-896.
- Negrelle, R. A. B. & Silva, F. C. (1992). Fitossociologia de um Trecho de Floresta com *Araucaria angustifolia* (Bert.) O. Ktze. No Município De Caçador-SC. Embrapa Florestas. *Boletim de Pesquisa Florestal*, Colombo, n. 24/25, p. .37-54, Jan./Dez.
- Negrini, M., Higuchi, P., Silva, A. C., Spiazzi, F. R., Buzzi Junior, F., Vefago, M. B. (2014). Heterogeneidade Florístico-Estrutural Do Componente Arbóreo Em Um Sistema De Fragmentos Florestais No Planalto Sul Catarinense. *Revista Árvore*, Viçosa-MG, v.38, n.5, p.779-786.
- Lima, T. E. O., Hosokawa, R. T., Machado, S. A. (2012). Fitossociologia do Componente Arbóreo de um Fragmento de Floresta Ombrófila Mista Aluvial no Município de Guarapuava, Paraná. *Floresta*, Curitiba, PR, v. 42, n. 3, p. 553 - 564, jul./set. 2012.
- Ribeiro, T.M., Ivanauskas, N. M., Martins, S. V., Polisel, R. T., Santos, R. L. R. (2013). Fitossociologia de uma Floresta Secundária com *Araucaria angustifolia* (Bertol.) O. Kuntze na Estação Ecológica de Bananal, Bananal-SP. *Floresta e Ambiente* 2013; 20(2):159-172 .
- Rondon Neto, R. M., Watzlawick, L. F., Caldeira, M. V. W., Schoeninger, E. R. (2002). Floristic and Structural Analysis of a Montane Mixed Ombrophylous Forest Fragment In Criú Va, RS – BRAZIL. *Ciência Florestal*, Santa Maria, v. 12, n. 1, p. 29-37.

- Sonego, R. C., Backes, A., Souza, A. F. (2007). Descrição da estrutura de uma Floresta Ombrófila Mista, RS, Brasil, Utilizando Estimadores Não-Paramétricos de Riqueza e Rarefação de Amostras. *Acta bot. bras.* 21(4): 943-955.
- Souza, R. F., Machado, S. A., Galvão, F., Figueiredo Filho, A. (2017). Phytosociology of Tree Vegetation in Iguaçu National Park. *Ciência Florestal*, Santa Maria, v. 27, n. 3, p. 853-869, jul.-set.
- Téo, S. J., Schneider, C. R., Demarco, L. F., da Costa, R. H. (2014). Comparação de Métodos de Amostragem em Fragmentos de Floresta Ombrófila Mista, em Lebon Régis, SC. *Floresta*, Curitiba, PR, v. 44, n. 3, p. 393 - 402, jul. / set.
- Viani, R., Costa, J., Rozza, A., Bufo, L., Pinho-Ferreira, M., Oliveira, A. (2011). Caracterização florística e estrutural de remanescentes florestais de Quedas do Iguaçu, Sudoeste do Paraná. *Biota Neotropica*. 11. 10.

APPENDIX C - SELECTION OF GLOBAL CIRCULATION MODELS (GCMS) AND ENVIRONMENTAL VARIABLES

To choose the GCMs for future projections in 2050, we aimed at the most dissimilar models to capture the climatic variation predicted for the region under the scenario SSP5-8.5. First, we selected 100 random points within the study region and extracted the climatic information from the 19 bioclimatic variables and all 9 GCMs available at the WordClim database. Then, we performed *non-metric multidimensional scaling* (NMDS) ordination, based on Euclidean distance to reduce the climatic variation to two dimensions. Finally, we plotted the NMDS ordination and drew a minimal polygon around the points, and an ellipse to represent the centroid of the points per group. We selected the GCMs that stood out from the rest of the group. They were the GCMs: BCC-CSM2-MR, CanESM5, CNRM-ESM2-1, MIROC-ES2L.

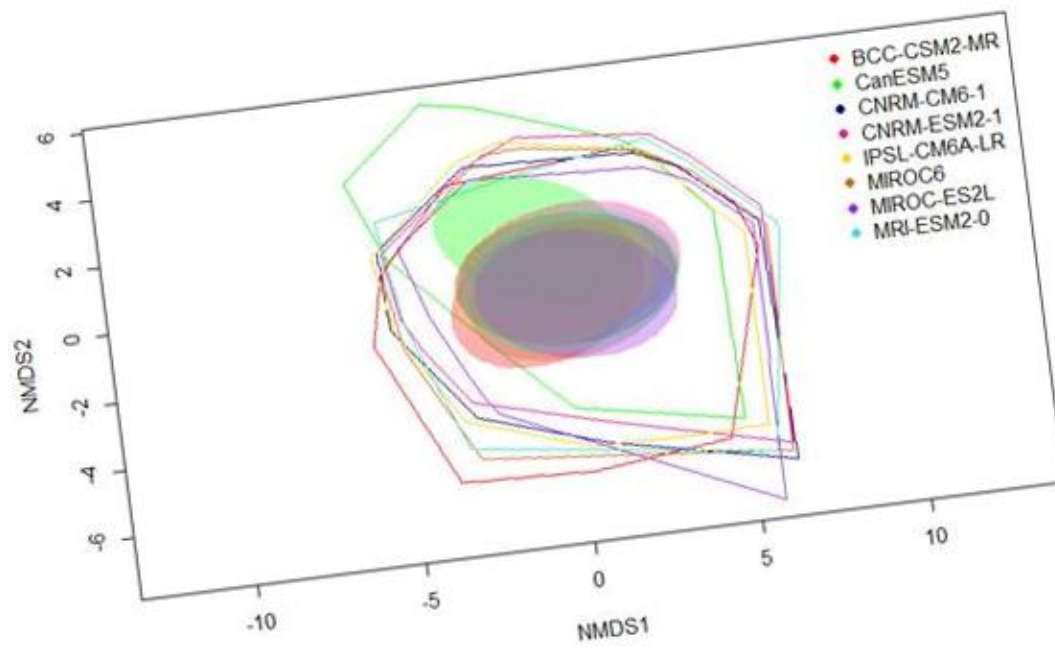


Figure 1. Appendix b. Two-dimensional plot of a *non-metric multidimensional scaling* representing the projected climatic variation for 2050.

APPENDIX D – SELECTION OF VARIABLES

We obtained bioclimatic layers from WorldClim v2.1 (<https://worldclim.org/>; Fick and Hijmans, 2017) and physical properties of soils from SoilGrid (<https://soilgrids.org>). In addition, we generated an Aspect Index and a Topographic Wetness Index (TWI) based on a digital elevation model in the SAGA GIS software (<http://www.saga-gis.org/>). Respectively, they indicate the directions the physical slopes face and the spatial soil moisture patterns. Both indices are commonly used to indicate microclimate conditions that can affect species distribution and vegetation patterns (Sørensen et al., 2006). All layers were at 2.5 arc-minutes resolution. To select variables for the niche modeling, we performed a Principal Component analysis (PCA) using the full set of variables from the current scenario to visually inspect the biplot and selected variables that were less correlated. We then performed a stepwise correlation analysis to detect pairs of variables with coefficient $|r| \geq 0.7$ and exclude the correlated variable with the greater variance inflation factor, using the function 'vifcor' from the usdm package (Naimi et al., 2014).

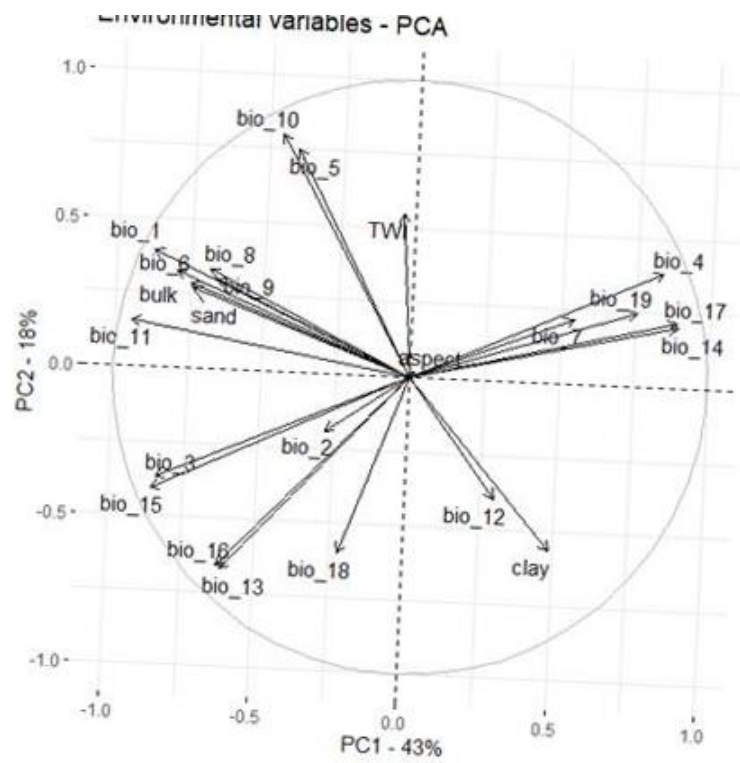


Figure 1. Appendix c. PCA plot from first process of variable selection. 19 environmental variables, 3 soil variables and 2 topographic variables.

APPENDIX E – SIMULATION TO DEFINE ACCESSIBLE AREA

Soberón and Peterson (2005) summarized the main factors that determine species' distribution into three components, the so-called BAM diagram: (B) biotic interactions and variables linked to resources; (A) abiotic or environmental factors; and (M) for movement or dispersal, representing the regions that have been accessible to the species. Species distribution is manifested in the intersection of these three components. We have estimated areas accessible to *Araucaria angustifolia* ("M") by applying a simulation process that considers habitat suitability, dispersal and colonization of individuals across the landscape over multiple cycles projected to Mid Holocene (MH) and Last Glacial Maximum (LGM) climates. We tested configurations of model parameters, environmental variables and occurrences points to reach a final configuration. The final accessible area was validated with palynological data (fossil pollen records) from the MH and LGM (Table appendix 1) available from Bergamin et al. (2019). We also constrained the final accessible area where the Pantanal ecoregion is currently distributed, assuming that it represents an important barrier that kept *Araucaria* from ever reaching and dispersing across the Andes despite the suitable conditions (Figure 3).

Palynological data from the mid holocene (mh) and last glacial maximum (lgm) used for validating estimation of accessible areas.

LGM		MH	
longitude	latitude	longitude	latitude

-50.1011	-29.0525	-50.1011	-29.0525
-55.2172	-29.5867	-55.2172	-29.5867
-45.5333	-22.7867	-45.5333	-22.7833
-44.5567	-22.7417	-44.5667	-22.7139
-48.6333	-26.0667	-42.2167	-17.95
-48.8814	-27.8967	-48.6333	-26.0667
-46.65	-23.9333	-45.9667	-23.2833
-50.6217	-29.493	-48.8681	-27.8967
-43.3667	-20.0833	-50.5489	-29.7458
		-50.5728	-29.4764
		-50.6217	-29.4931

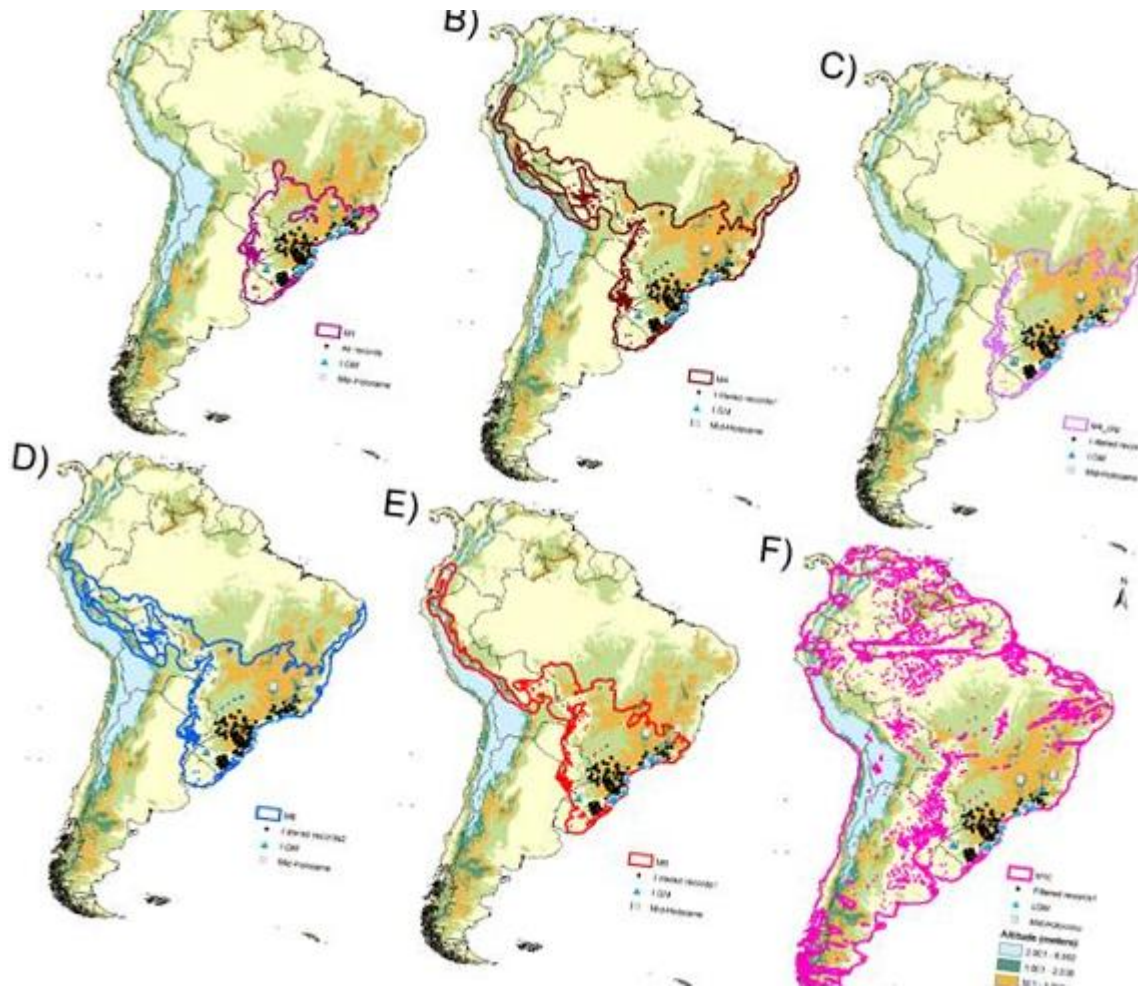


Figure 1. appendix C. A) no filter + climate set 1 (bio1, 5, 12, 13, 14); b) filter 1 (+ climate set 1; c) clipped version of figure b assuming pantanal as a barrier; d) filter 2 + climate set 1; e) filter 1 + climate set 2 (bio 7, 9, 12, 17, 18); f) filter 1 + climate set 2 + soil (bulk density, weight % of sand, topographic wetness index). The final accessible area is represented in panel “c”.

APPENDIX E - MODEL COMPARISON AND SELECTION

Performance of the 10 best models for *Araucaria angustifolia* selected based on statistical significance estimated via partial ROC (ROC_P), prediction ability (Omission Rate at 5%) and model complexity (AICc). (FC) represents the combination of feature classes ("l" linear, "q" quadratic, "p" product). The final model selected based on the above criteria is marked with an asterisk (*).

Model	FC	ROC _P	Omission rate 5%	Variables	Δ AICc	W AICc
Model 1	lq	<0.001	0.051	bio 7, 13, 17, bulk, TWI	0	0.219
Model 2	lq	<0.001	0.077	bio 7, 12, 13, 17, bulk	2.03	0.080
Model 3	lq	<0.001	0.077	bio 17, 12, 13, 17, bulk, TWI	2.85	0.053
Model 4	lqp	<0.001	0.102	bio 7, 13, 17, bulk, TWI	3.21	0.044
Model 5*	lq	<0.001	0.026	bio 3, 7, 12, bulk, TWI	3.40	0.039
Model 6	lq	<0.001	0.051	bio 7, 13, 17, bulk, TWI	3.50	0.037
Model 7	lq	<0.001	0.077	bio 7, 12, 13, 17, bulk, TWI	3.51	0.038
Model 8	lq	<0.001	0.077	bio 7, 12, 13, bulk, TWI	3.80	0.038
Model 9	lq	<0.001	0.077	bio 7, 12, 13, 17, bulk	4.36	0.033
Model 10	lq	<0.001	0.051	bio 7, 13, 17, bulk	4.50	0.025

Variable importance: bio 3=0.24; bio 7=0.89; bio 12=0.55; bio 13= 0.85; bio 17=0.77; bulk=1.00; sand=0.19; TWI=0.72

Omission rate 5% indicates the proportion of test localities that falls into pixels not predicted as suitable for the species, discarding 5% of test localities at the lowest suitability (Phillips *et al.*, 2006). The lowest values indicate good performance.

Variable importance is presented as the sum of Akaike weights (W AICc) across models with a given variable. bio 3: Isothermality; bio 7: Temperature Annual Range; bio 12: Annual Precipitation; bio 13: Precipitation of Wettest Month; bulk: soil bulk density; sand: weight percentage of sand particles in the soil; TWI: topographic wetness index

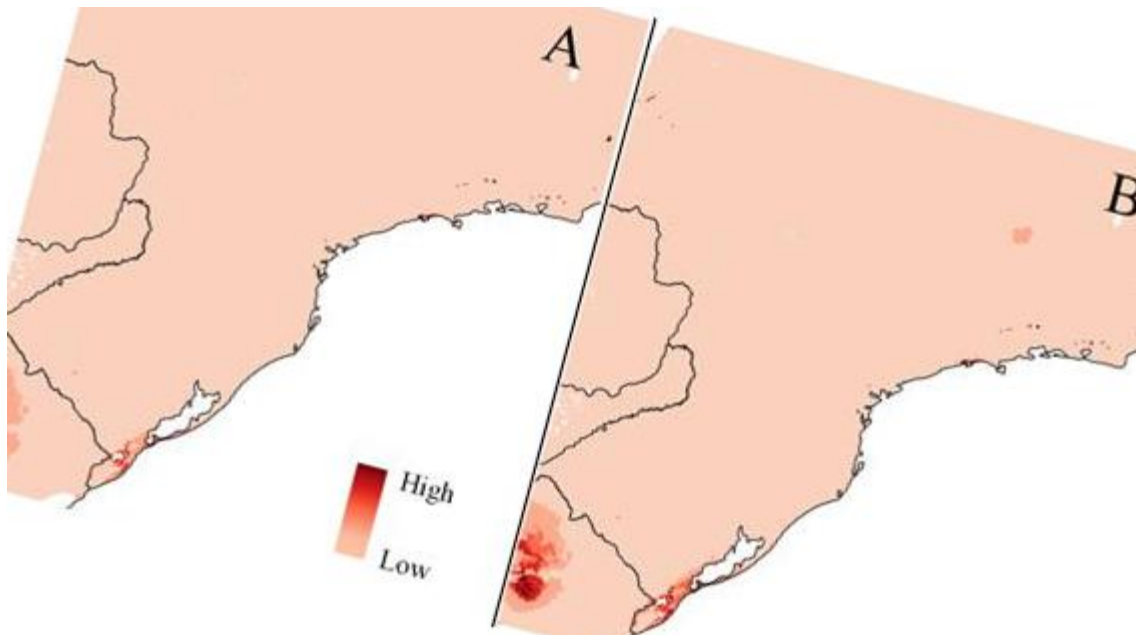
APPENDIX F – MOP ANALYSES

Figure 1. appendix G. Extrapolation risk of model output in future projections in two different scenarios (MOP results).

APPENDIX G – POTENTIAL DISTRIBUTION

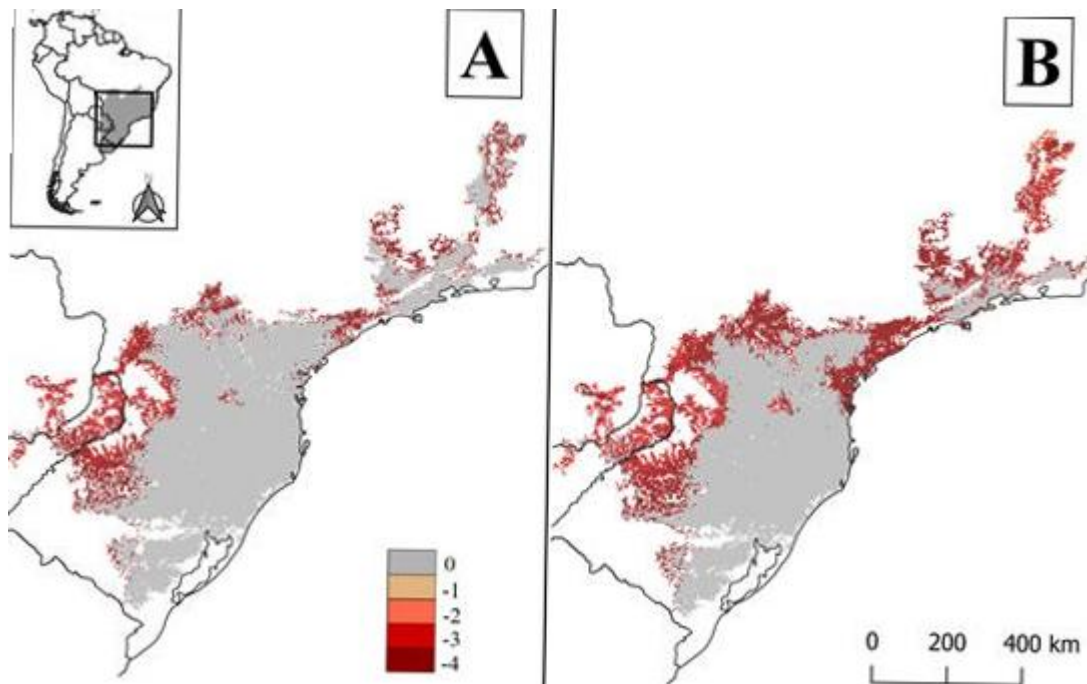


Figure 1. appendix G: Potential distribution loss of *Araucaria angustifolia* in 2050 compared to present under scenarios SSP2-4.5 (A) and SSP5-8.5 (B). Numbers -1 to -4 indicate suitability loss: (-4) four GCMs; (-3) three GCMs; (-2) two GCMs; (-1) one GCM. Stable areas in all GCMs are indicated by grey (0).

CONCLUSÕES E RECOMENDAÇÕES

Deve-se observar que, comparado a artigos relacionados à modelagem da Araucária, nossos resultados se distanciam de estudos que preveem a extinção da espécie nos próximos. Contudo, chegam a conclusões semelhantes quanto a retração da espécie para a região sul para áreas de campo. Os pontos de Ocorrência de Araucárias no Sul do Rio Grande do Sul ajudam o modelo a identificar áreas de ocorrência nessa região e adicionam novas informações ambientais para a distribuição da espécie. O modelo também apontou que, quanto a necessidade da preservação da Araucaria, ainda há muito a ser planejado, e vista que, no futuro muitas AP deixarão de atender a sua área de distribuição. Além disso, a espécie também possui área de distribuição que, no futuro, não possui remanescentes florestais, com isso conclui-se que além da preservação, que ainda há a possibilidade da realização de muitos trabalhos de restauração e reflorestamento.

Este estudo tinha como objetivo a modelagem de uma espécie icônica de grande importância ecológica e cultural, através de metodologias que não foram realizadas anteriormente, como a utilização de um pacote recente, o uso de uma área de estudo modelada baseada em princípios biológicos, a utilização de novos cenários (SSP) do Wordclim, e seus novos GCMs (atualizados em 13 de março de 2020), e por final discutimos o tópico das incertezas do modelo, temática que é ainda pouco explorada no estudo da Modelagem de Nicho Ecológica.

Além disso, obtivemos pela utilização de variáveis ambientais, além das climáticas, como de solo, e topográficas, e estas se provaram ter alto valor de significância para a criação de um modelo mais robusto quando se trata do estudo da *Araucaria angustifolia*. Somado a isso, avaliação dos modelos que levam em consideração *omission rate*, *partial ROC* e *model complexety* tem alto grau de confiabilidade. Os baixos graus de incerteza dentro da área de previsão do modelo, corroboram com essa afirmação.

Idealmente, para se melhor concluir o tema, outras metodologias deveriam ser redigidas e comparadas, especialmente às que se referem ao uso de diferentes algoritmos, e comparações e médias entre seus resultados. Deve-se reforçar também a importância de, em estudo futuros, considerar com maior profundidade fatores bióticos ainda não analisados.